

Male Nest Defense in the Digger Wasp *Cerceris binodis* (Hymenoptera: Sphecidae)

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Abstract.—Male *Cerceris binodis* (Hymenoptera: Sphecidae: Philanthinae) defend territories that contain nesting females from conspecific males. A female which is provisioning a nest will mate when she returns to the nest and a male is present. This mating system represents the first description of male nest defense in the genus *Cerceris*. Presumably, this behavior occurs in *C. binodis* because females nest in aggregations, and mate multiply.

INTRODUCTION

The cosmopolitan genus *Cerceris* contains over 800 species (Bohart and Menke 1972), more than any other sphecid genus, but mating systems of relatively few *Cerceris* species have been studied. Non-resource based territoriality has been reported in all *Cerceris* mating systems which have been described (Alcock 1975a, Evans 1971, Evans and O'Neill 1985, Evans and O'Neill 1988), and in four other genera in the sphecid subfamily Philanthinae: *Aphilanthops*, *Philanthus*, *Clypeadon*, and *Eucerceris* (Evans and O'Neill 1988; O'Neill 1990). In this mating system, males apply volatile secretions originating from mandibular glands to a substrate with clypeal brushes, and defend these non-resource based territories from conspecific males. Philanthine females typically nest in dispersed conditions, mate once at the beginning of the nesting period away from the nest, presumably are attracted to mandibular gland secretions, and enter territories to copulate (Evans and O'Neill 1988). The mating system of *C. binodis* departs from these conditions. Females nest in aggregations, and mate multiply at the nest. Resident *C. binodis* males stand on or directly adjacent to nests, exclude conspecific non-resident

males from nests, and do not scent mark territories. Of the eight philanthine genera, male nest defense has been described only in *Philanthus*, and presumably is derived within that genus (Evans and O'Neill 1988). Male nest defense is described here for the first time in the genus *Cerceris*, and also presumably represents a derived condition within this taxon.

METHODS

An aggregation of nesting *C. binodis* females was discovered on Barbour Lathrop trail on Barro Colorado Island, Republic of Panama on July 8, 1994. A group of five nests that were close enough together to be observed simultaneously were marked with numbered tags. Male and female wasps were individually marked with enamel paint on the thorax, and head widths were measured to the nearest 0.05 mm with Manostat calipers. The nests were observed on two days after individuals were marked. Observations were made from 1355-1525h on the first day, and from 1515-1650h on the second day. The behaviors recorded were the amount of time that males spent standing on or adjacent to nests, defensive interactions between males, and copulations.

RESULTS

When a female returned to a nest with prey, and a resident male was present, she would land on the nest tumulus, and copulate. However, a female would fly directly into her nest if no male was present. This behavior is also described in the sphecid genus *Oxybelus* (Crabroninae) (Peckham et. al. 1973). Females were provisioning nests in all cases where males defended nests and mated. Not only did males defend nests while females were on provisioning trips, but on two occasions, a male was observed to defend a nest while the female was inside the nest. These males were observed to bite at the females, and attempted to pull them out of the nest with their mandibles. One of these males mated with the female when she exited the nest.

Nest defense duration was determined by the length of time a resident male was either in contact with a nest, directly adjacent to a nest, or defending a nest from non-resident males. On day one, males YB, RB and BY, spent a total of 66.7, 21.1, and 12.2 percent of the observation period defending nests, respectively. On day two, males WRB, YB, RY, BB and RB spent a total of 67.3, 41.1, 16.8, 1.2 and 0.8 percent of the observation period defending nests, respectively. Males YB and WRB obtained 71% (5/7) of the observed copulations, and there is a positive correlation between the duration of time which males defend nests and the number of copulations that males obtain; $r = 0.86$.

At times, multiple males were simultaneously defending different nests in the aggregation. Male-male interactions were considered a territorial defense when a resident male flew from his nest to chase a non-resident male. These chases rarely ended in grappling on the ground; otherwise, there was no physical contact. Forty eight aggressive interactions were recorded between resident and non-resident males. Resident males won significantly

more (95%) interactions than non-resident males (Chi-square = 40.1, $df = 2$, $P < 0.001$). In 11 of the 48 interactions, identity and size of both males were known; resident males won 7 of these 11 interactions. Mean head widths of winner and loser males were 3.83mm and 3.76mm, respectively. The difference in mean headwidths between winner and loser males is not statistically significant (t-test = .82, $df = 20$, $P > 0.4$).

DISCUSSION

Size has been demonstrated to determine dominance in territorial sphecids such as *Philanthus* (O'Neill 1983a, b), and in many other insect mating systems (Thornhill and Alcock 1983). In *C. binodis*, however, territory ownership, not size, apparently determines dominance (one should note the small sample size ($n=11$) where identity of both males was known). This phenomenon has also been demonstrated in other insect mating systems (Davies 1978, Eickwort and Ginsberg 1980, Wang and Greenfield 1991). Data also indicate that as the total time invested in nest defense per male increases, the number of copulations obtained per male also increases. This is not surprising, since females mate with the resident male which is defending her nest.

In many *Cerceris* species, females nest in aggregations, but males do not defend nests from conspecific males. The requirement which is likely responsible for the difference between the mating systems of these species and *C. binodis* is that *C. binodis* females retain their receptivity after the initial mating. This might maintain male territoriality, particularly if there is last male sperm precedence (Hook and Matthews 1980, Brockmann and Grafen 1989). However, males in several species of *Philanthus* defend territories which contain nesting females that do not display continuous receptivity (Gwynne 1980, Evans and O'Neill 1988). Data collected from this study do not indicate that fe-

males are continuously receptive throughout the nesting period, only that they mate multiply. In addition, last male sperm precedence is not demonstrated in this species, but often occurs in insects (Thornhill and Alcock 1983).

CONCLUSION

This is the first description of male nest defense in *Cerceris*. This derived mating system shows striking convergence with the mating systems of both *Oxybelus* (Peckham et. al 1973, Hook and Matthews 1980), and *Philanthus* (Evans and O'Neill 1988) species. Moreover, *C. binodis* males do not scent mark territories, and their clypeal brushes are reduced. Since clypeal brushes are a synapomorphy of Philanthinae, and are present in most species of *Cerceris* (Alexander 1992), reduction of the clypeal brushes in *C. binodis* represents a derived condition. Evans and O'Neill (1988) state that scent marking occurs in all territorial philanthines where the mating systems have been described. Therefore, this mating system represents an exception to their statement (see also Alcock and Gamboa 1975).

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